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XII

MECHANISM IN THE PRODUCTION OF THE THROAT-FAN IN THE FLORIDA CHAMELEON, ANOLIS CAROLINENSIS[1]

BY CHAS. E. VON GELDERN

I

The production of the throat-fan in the Florida Chameleon (*Anolis carolinensis*), is, aside from the remarkable cutaneous color changes, one of the most striking features of this lacertilian.

The distended throat-fan, dewlap or gular pouch, which is best developed in the males, is a thin fold of skin attached along the mid-ventral line of the throat. It is somewhat semicircular in outline and extends from the intersection of the mid-ventral line and a line drawn at right angles passing through the eyes, to a variable distance on the chest.

The color of the distended fan varies from a delicate pink to a bright vermilion and, on closer observation, is spotted with scattered white scales.

When the fan is retracted, the skin on the throat is loose and arranged in longitudinal folds. It is white in appearance with minute longitudinal red, linear markings. The scales are prominent and appear as small, laterally depressed cones.

[1] The dissection of Anolis was made in the department of Anatomy of Tulane University. The comparative work was done in the department of Zoology at Stanford University. I am indebted to Professor J. O. Snyder for the material used in dissection.

It is evident that in distending the fan, the folds flatten out and the closely approximating scales become more or less separated, showing the pink or vermilion epidermis between them.

The fan is distended frequently and during various emotional states. It is a common observation to see one of the lizards sitting on a branch or fence rail, suddenly rise up on its front legs, distend the fan and accompany this by a quick succession of up-and-down motions produced by flexing and extending the front legs. No purpose for the act is apparent since the animal is undisturbed by outside influences.

A male Anolis will, upon spying a female, bob up and down and distend his fan with great frequency as if he were displaying himself to his greatest advantage.

Two males in combat will keep their fans distended, rise up on their toes, flatten out their bodies from side to side, and erect a fold of skin along the midline of the back of the neck. The usual appearance of the animal is thus markedly changed, even the prominent eyes, with their visible yellow irises, recede and appear as black beads. With grotesque, lateral swaying motions the combatants slowly encircle one another, each awaiting an opportunity to make a final rush and end the struggle victoriously. When one of these lizards is captured and held in the hand it will attempt to bite in a most vicious manner and distend the fan at the same time.

II

The underlying mechanism in the production of the fan is the hyoid apparatus, as has been stated by Ditmars, Gadow, Chemin, Bronn and others. None of these authors except Chemin has, as far as I have been able to ascertain, described the mechanism and the forces employed.

For the purposes of description the hyoid apparatus of Anolis may be divided into a basi-hyal; anterior extension or processus entoglossus; third horn of Chemin, posterior horn of Huxley or the processus retrobasalis; anterior horns, lesser horns or cerato-hyals and the posterior horns, middle horns of Huxley, greater horns, cerato-branchials or thyro-hyals. (Fig. 1 A.)

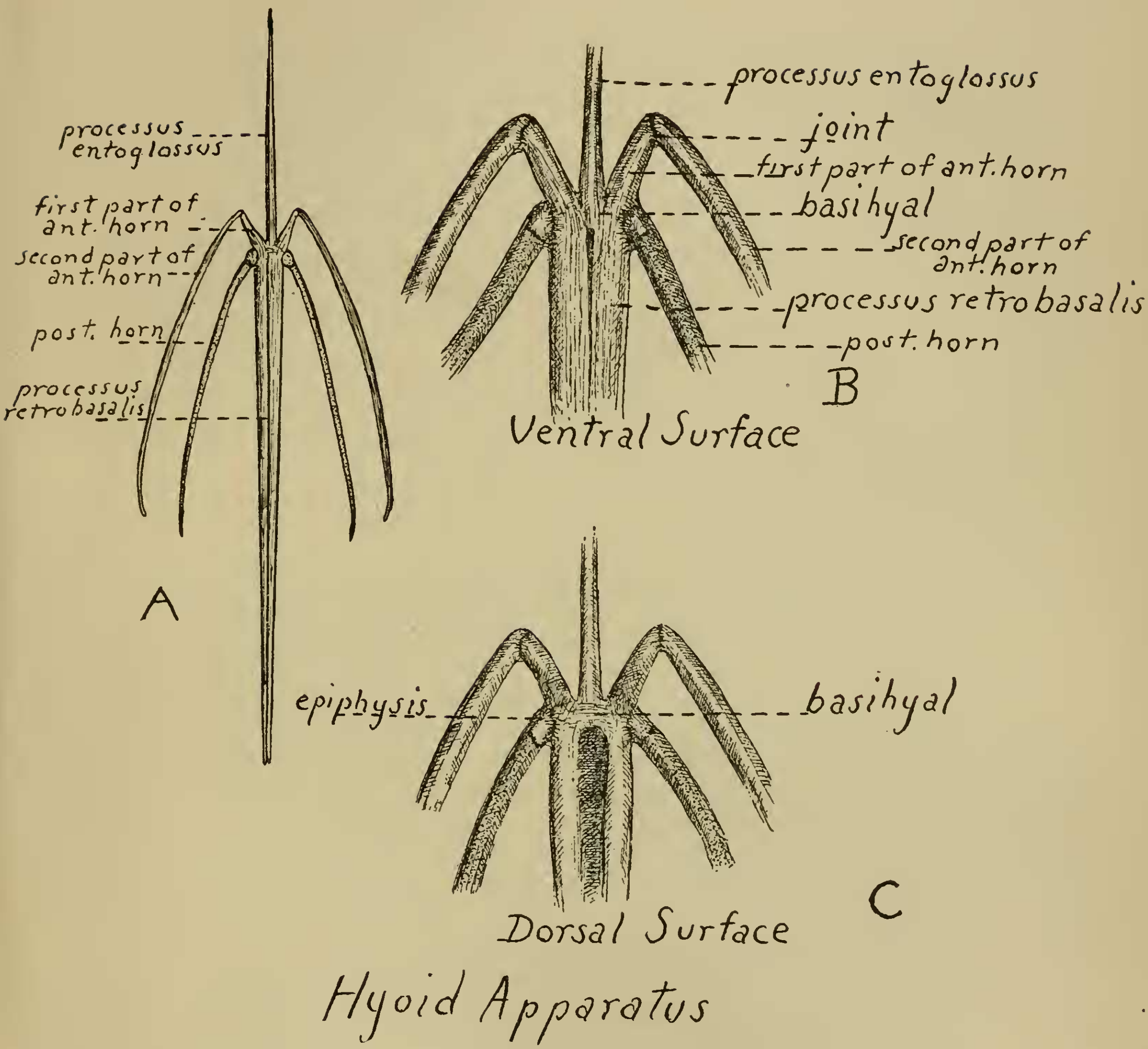


Fig. 1 A, B, C

By the body or basi-hyal is meant that part to which the other structures attach. This is a small bar of cartilage with a slight concavity dorsally. It measures about 1 m.m. in length and about .5 m.m. in thickness. (Fig. 1 A, B, C.)

Arising from the middle of the cephalic border is the processus entoglossus or anterior extension. This is a fine, tapering, cartilaginous rod. It measures about 8 to 10 m.m. in length and ends in a fine point. (Fig. 1 A.)

From each extremity of the body and extending caudally, arises the paired processus retrobasalis or the posterior horns (Huxley). These are fairly firm, cartilaginous rods which gradually taper to a fine point at their caudal extremity. They are 18 to 22 m.m. in length. Near the cephalic extremity they lie in close approximation showing a groove dorsally between them but only a fine slit ventrally. They are bound together by firm connective tissue. More caudally the distinction between the dorsal and ventral aspect is lost. They closely approximate each other, yet are easily separated with a teasing needle. These cartilages are rather stiff in their cephalic third but become more and more flexible distally. (Fig. 1 A, B, C.)

The anterior horns or cerato-hyals arise from the extremities of the body or basi-hyal with which they are continuous. They are divided into two parts which are separated by a movable joint. (Fig. 1 A, B, C.) The first part, which is continuous with the body, is a short, tapering, cartilaginous rod measuring 1.5 to 2 m.m. and terminating bluntly. It runs cephalad, laterad and slightly dorsad. The angle formed by it and the corresponding horn is about 60 degrees. The second part, also cartilaginous, is attached to the first by a joint capsule allowing fairly free movement. This part extends laterad and caudad, tapering as it approaches its extremity, thence curving dorsad. With the first part it forms an angle of about 75 degrees. (Fig. 1 A, B. C.)

The posterior horn, middle horn (Huxley) or cerato-branchial articulates with the basi-hyal at the junction of the anterior horn and the processus retrobasalis. This structure is a fine, tapering, osseous rod, measuring 12 m.m., with a rounded, cartilaginous epiphysis at the proximal extremity and a pointed epiphysis at the distal extremity. There is a medullary cavity in the compact bone. The joint formed with the basi-hyal is surrounded by a fibrous capsule allowing a great range of motion. This horn runs nearly parallel with the posterior part of the anterior horn. (Fig. 1 A, B, C.)

III

The basi-hyal lies in the midline just caudad to the larynx and base of the tongue, being intersected by a line running through the eyes. It is covered by skin, superficial fascia and the thin, superficial mylohyoid. (Fig. 2.)

The processus entoglossus lies deeply embedded between the extrinsic muscles of the tongue and terminates near the symphysis of the jaw. (Figs. 2, 3, 4.)

The anterior horn lies beneath the suprahyoid and hyoglossus muscles, crosses the pterygoid muscle, thence curving around the mandible and ending in a mass of connective tissue just caudal to the ear. (Fig. 2.)

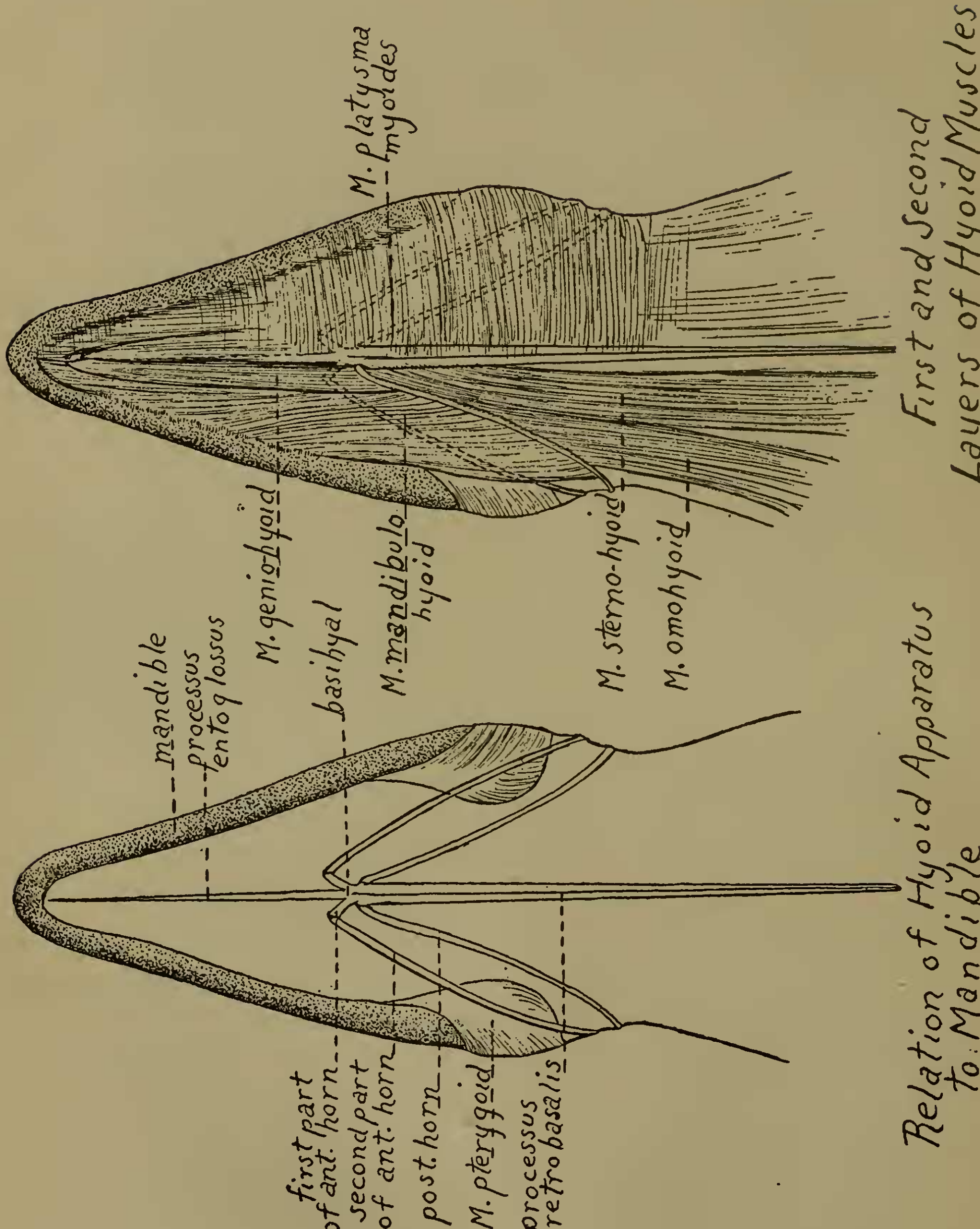
The posterior horn is more superficial, being covered in part by the thin mylo-hyoid only. Distally it curves over the side of the neck just caudad to the mandible, ending in the superficial connective tissue. (Figs. 2 and 3.)

The processus retrobasalis is superficial, being embedded in loose connective tissue just beneath the skin. It lies in the midline and extends to the chest wall. (Figs. 2 and 3.)

The hyoid apparatus forms a typical lever of the first class. The fulcrum is at the junction of the basi-hyal and the posterior horn. The short arm of the lever, which is the power arm, is the first part of the anterior horn. The processus retrobasalis forms the long arm. (Fig. 1 A.)

A force exerted from the extremity of the anterior horn or short arm in a caudal direction, will, due to a slight dorsal inclination of the latter, cause it to swing dorsad and caudad, thus rotating the body at the fulcrum and swinging the horizontal processus retrobasalis through an arc of 90° in a cephalad and ventrad direction, to assume a vertical position. Necessarily the force must be equally applied to the first part of both horns. The second part of the anterior horns and the posterior horns act as supports and tend to prevent any lateral displacement of the long arm of the lever during its assumption of the vertical position.

Necessarily the processus entoglossus would, on meeting the resistance of the tongue during the rotation of the body, be bent dorsally, but its extreme flexibility renders this possible.

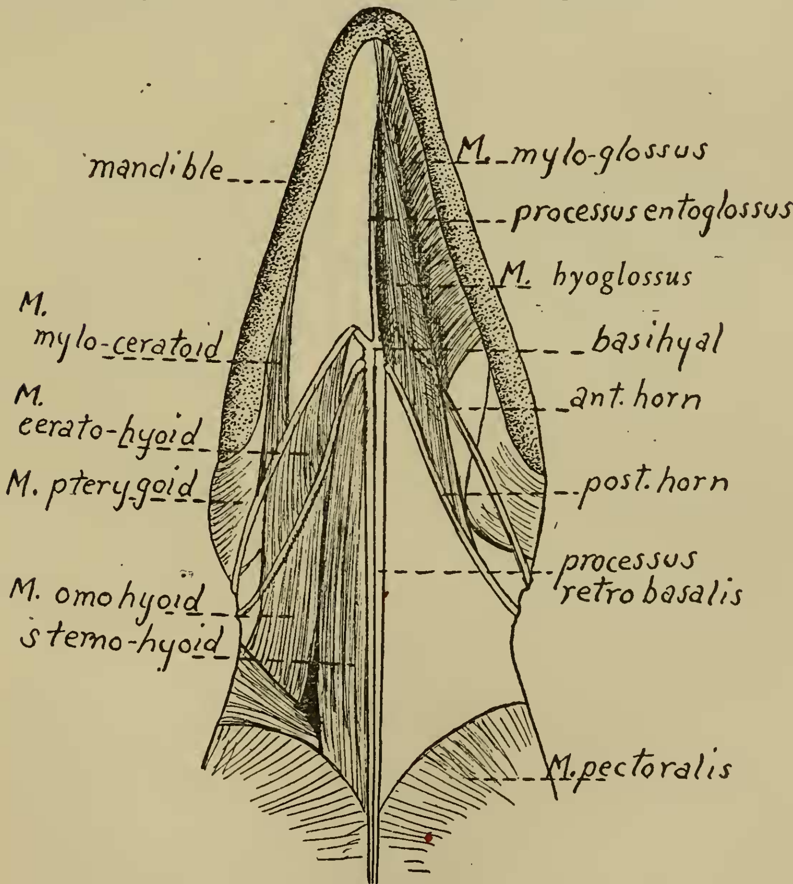

mandible
processus entoglossus
basihyal
first part of ant. horn
second part of ant. horn
post. horn
M. pterygoid
processus retrobasalis
Relation of Hyoid Apparatus to Mandible
M. geniohyoid
M. mandibulo-hyoid
M. sterno-hyoid
M. omohyoid
M. platysma myoides
First and Second Layers of Hyoid Muscles

Figs. 2 and 3

In order that the muscular forces necessary to erect the processus retrobasalis be understood, it is necessary to take up the individual muscles of the hyoid apparatus.

IV

These muscles are arranged in three layers. First, there is a thin, superficial layer not directly connected with the hyoid. Secondly, there are the supra- and infra-hyoid muscles, and thirdly, the muscles of the tongue. (Figs. 3, 4.)



Third Layer of Hyoid Muscles

Fig. 4

The mylo-hyoid or platysma myoides is poorly developed in Anolis and is visible only under the dissecting microscope or in microscopical cross sections. It is a thin sheet having its origin along the mandible and inserting in a median raphe. (Fig. 3.)

The second layer consists of four muscles, namely, the genio-hyoid, mandibulo-hyoid, sterno-hyoid and omo-hyoid. (Figs. 3, 4.)

The genio-hyoid is a thin strip of muscle tissue extending from its origin, just lateral to the symphysis, to its insertion on the posterior horn of the hyoid, near its junction with the body. It tends to pull the hyoid cephalad, or, if the latter be fixed, assists in opening the jaw.

The mandibulo-hyoid is a thin sheet of muscle tissue having its origin along the inner aspect of the anterior two-thirds of the mandible interdigitating with the mylo-hyoid and inserting along the posterior horn of the hyoid. It tends to pull the hyoid cephalad and dorsad, or, if the latter be fixed, it also assists in opening the jaw.

The sterno-hyoid takes its origin from the upper extremity of the sternum and inserts on the medial third of the posterior horn of the hyoid and proximal portion of the processus retrobasalis. It pulls the hyoid caudad and at the same time slightly ventrad. If the processus retrobasalis be vertical it pulls it back to a horizontal position. (Figs. 3, 4.)

The omo-hyoid takes its origin from the upper border of the scapula and inserts along the middle third of the posterior horn. It pulls the scapula cephalad and ventrad if the posterior horn be fixed. If the scapula be fixed, it pulls the posterior horn caudad. (Figs. 3, 4.)

If both the supra- and infra-hyoid group act simultaneously, the posterior horn is raised ventrad and firmly fixed. The basi-hyal is thus also raised ventrad, allowing a greater freedom of rotation. This action was noted in lizards under anesthesia, in which the muscles were exposed.

The third layer consists of the mylo-ceratoid, cerato-hyoid, hyoglossus and mylo-glossus. The mylo-ceratoid takes its origin near the middle of the inner aspect of the mandible, thence running over the pterygoid and inserting along the middle third of the second part of the anterior horn of the hyoid. It tends to pull the anterior horn cephalad after the latter has been pulled caudad by the cerato-hyoid. (Fig. 5.)

The cerato-hyoid takes its origin from the medial two-thirds of the second part of the anterior horn. Its fibres run almost directly caudad and insert along the posterior horn, except for about one-sixth of the proximal and distal ends. This muscle pulls the first part of the anterior horn caudad and dorsad, thus rotating the body at the fulcrum and swinging the processus retrobasalis cephalad and ventrad. (Fig. 4.)

The hyoglossus takes its origin along the posterior horn except for one-sixth of the distal end. The fibres converge and form a rounded belly which inserts along the inferior surface of the tongue by attachments to the intrinsic muscles. This muscle pulls the tongue backwards.

The mylo-glossus has a common origin with the mandibulo-hyoid along the inner aspect of the anterior two thirds of the mandible. It inserts along the side of the tongue. Its fibres run medio-caudad so that besides pulling the tongue from side to side when acting independently, it may be protruded when it acts with the one on the opposite side. (Fig. 4.)

V

In the distension of the throat fan the elastic skin of the throat is raised by the raising of the processus retrobasalis from the horizontal to the vertical position. The thinness of the distended fan is due to the cohesive quality of the two moist, opposing surfaces of skin, as well as atmospheric pressure. Its semi-circular outline is due to the tapering cartilages which, near their proximal end, are able to resist the elasticity of the skin but are unable to do so at their distal part, owing to increased flexibility.

The assumption of the vertical position by the processus retrobasalis from the horizontal, is due to the contraction of the cerato-hyoids which pulls the first parts of the anterior horns dorsad and caudad and causes the seconds parts of the anterior horns to slide caudad and laterad. At the same time, the basi-hyal is raised by the pull of the sterno-hyoids on the posterior horns. The entire apparatus is steadied by the antagonistic action of the mandibulo-hyoids and genio-hyoids

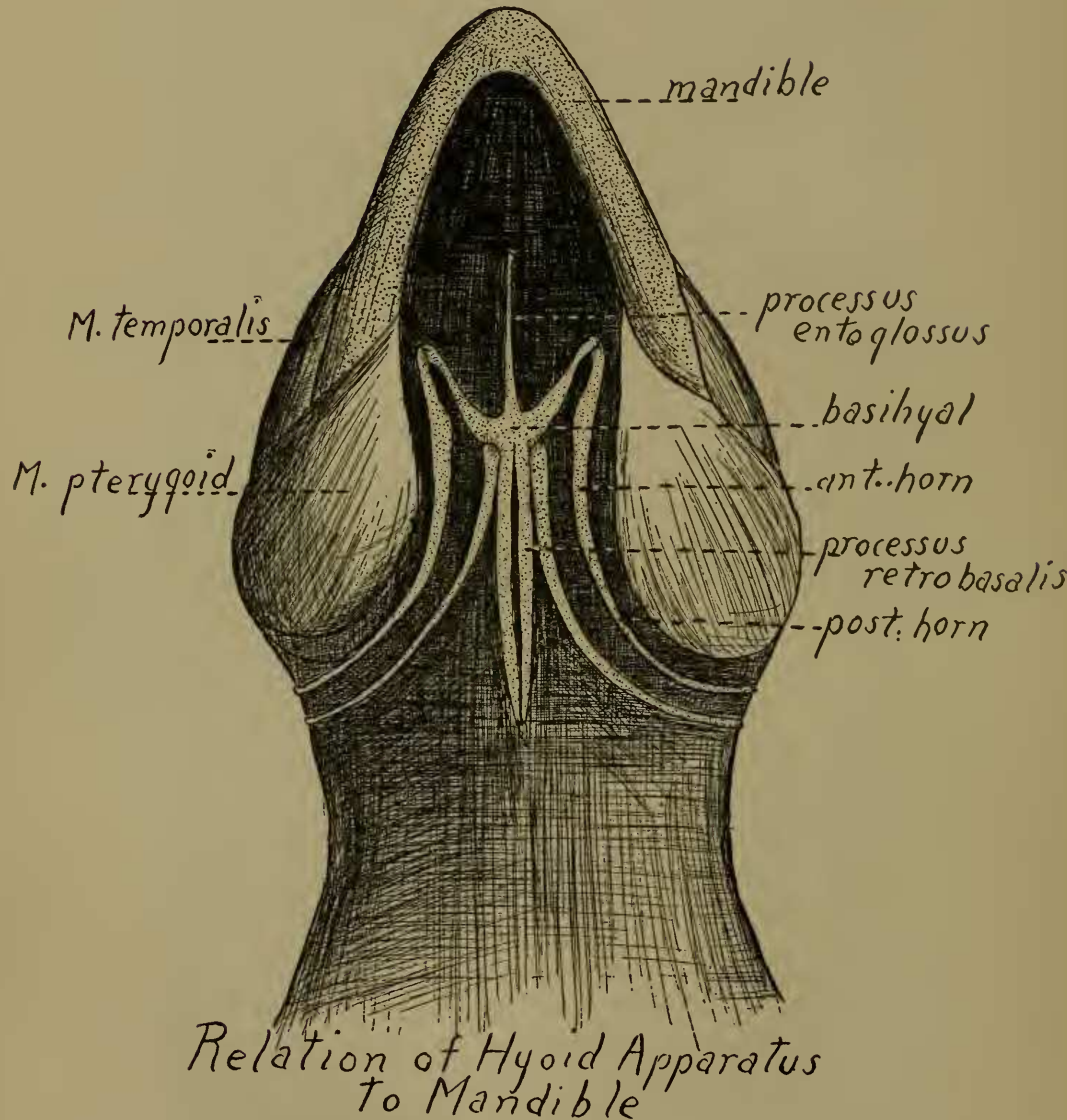

mandible
processus entoglossus
M. temporalis
basihyal
M. pterygoid
ant. horn
processus retrobasalis
post. horn
Relation of Hyoid Apparatus to Mandible

Fig. 5

on the posterior horn, against the pull of the sterno-hyoid and omo-hyoid. In this way the fulcrum is fixed. The muscles of the tongue probably play a small part in the action.

The retraction of the fan is accomplished by the elasticity of the skin, the contraction of the fibres of the sterno-hyoid, inserting on the processus retrobasalis and the pulling of the anterior horns cephalad by the mylo-ceratoids. The elasticity and spring of the entoglossus probably also aids to some extent.

For purposes of comparison, a dissection was made of the hyoid apparatus of a large Iguana. (Figs. 5, 6, 7.) With the exception of a well developed mylo-hyoid and for the reason that none of the muscle fibres of the sterno-hyoid insert on the processus retro-basalis, the structures were essentially the same.

VI

Some difficulty was encountered in naming the muscles of the hyoid apparatus. There was a question as to whether the nomenclature of the earlier investigators should be retained or whether these muscles should be given the names of homologous structures in the mammalia. If the old names be retained, which should be chosen among the various synonymous terms? If the muscles be named after mammalian homologues another difficulty arises, for the names of muscles in the mammalia usually represent the definite origin and insertion and consequently the name may lose its significance and become absurd when applied to a reptile in which there is a different origin and insertion. It was finally decided to retain for the most part the older nomenclature and leave the question for further investigation. (See list of synonyms.)

The same difficulty arose over naming the various structures of the hyoid apparatus. Again the older names were retained with the exception of the processus retrobasalis. This structure is called the posterior horn by Huxley, but since this would necessitate the changing of the name of the true posterior horn to middle horn, it was thought best to designate it by a new name. That it is part of the basi-hyal and not a true horn is evident by following its embryological development.

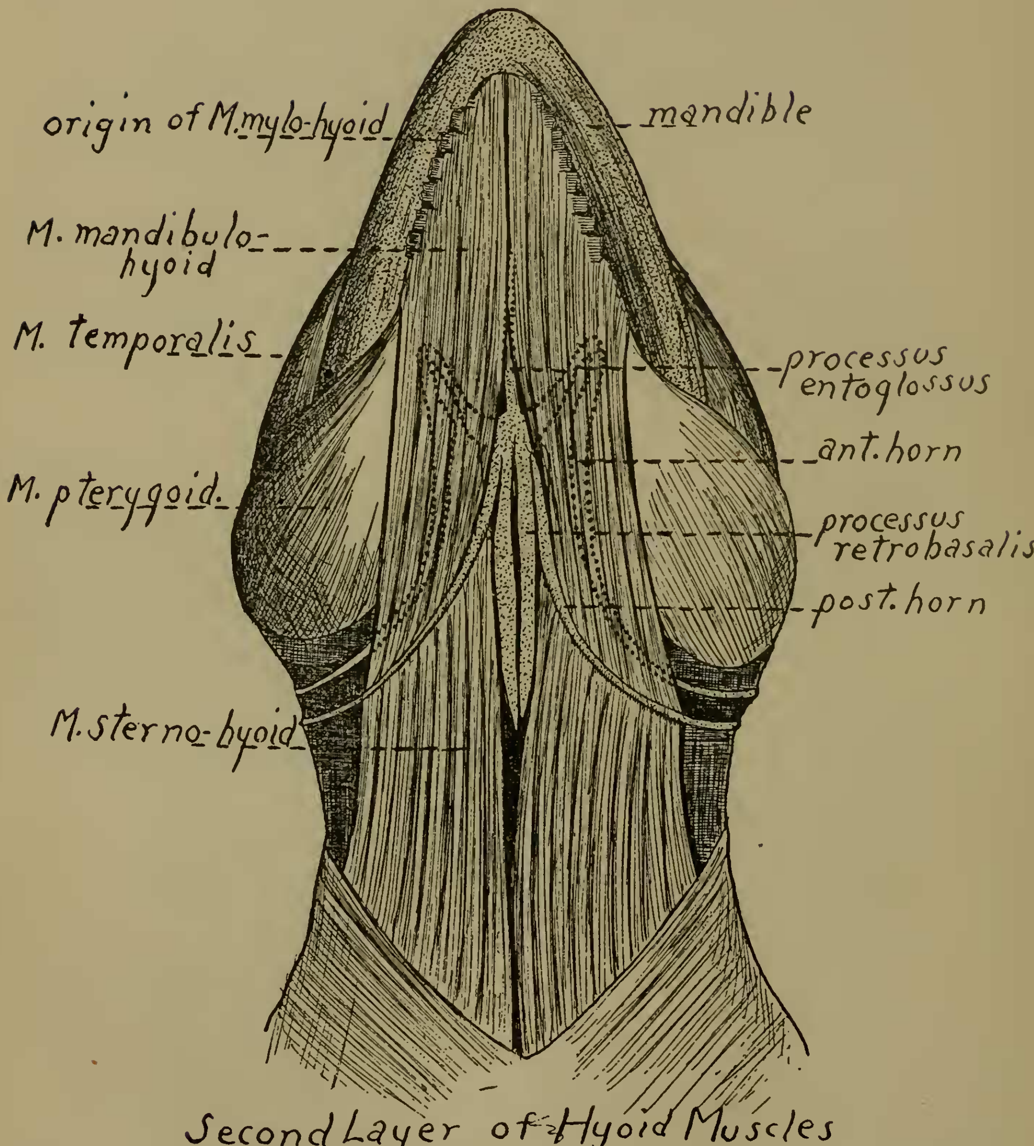

origin of M. mylo-hyoid
mandible
M. mandibulo-hyoid
M. temporalis
processus entoglossus
ant. horn
M. pterygoid.
processus retrobasalis
post. horn
M. sterno-hyoid
Second Layer of Hyoid Muscles

Fig. 6

VII

I was unable to find any literature on the hyoid apparatus of Anolis, but Dr. A. Chemin gives a good description of the hyoid apparatus and its relation to the throat-fan in *Colotes versicolor*. From the drawings in his paper there is a similarity between the hyoid apparatus of Colotes and Anolis, but the action varies markedly. Chemin considers the hyoid apparatus as a lever of which the basi-hyal forms the fulcrum, the processus entoglossus the power arm, and the processus retrobasalis the weight arm. He believes that the processus retrobasalis is made to swing cephalad and ventrad by pressure exerted in the dorsal direction on the processus entoglossus. This pressure is brought about by the pulling of the basi-hyal ventrad by means of the sterno-hyoids and since the processus entoglossus is prevented from moving ventrad with the basi-hyal because of a band of tissue extending from one hyoglossus to the other, the basi-hyal would rotate as the fulcrum and swing the processus retrobasalis forward. The cerato-hyoids simply pull on the anterior horns and increase the angle between the first and second parts. Chemin states that preceding the distension of the fan the animal swallows air and distends its dilatable pharynx.

Evidently then, according to Chemin, the greater the distension of the fan the greater must be the ventral excursion of the basi-hyal, since that is the only way in which pressure can be brought to bear on the processus entoglossus or the power arm of the lever. The anterior and posterior horns merely act as braces.

It is also evident that in Colotes the most important muscles are the sterno-hyoids, since these pull the basi-hyal ventrad. The cerato-hyoid plays a minor and insignificant part.

I have no desire to contradict the conclusions of Chemin on the mechanism of the production of the throat-fan in Colotes, but I cannot agree with the general statement that the mechanism in Colotes is essentially the same for all the Iguanidæ. Certainly it differs markedly in Anolis where the processus entoglossus is not the arm of the lever and only acts as a hindrance to the production of the throat-fan. In Anolis the cerato-hyoids play the most important role and the sterno-hyoids a minor role. Furthermore, the production of

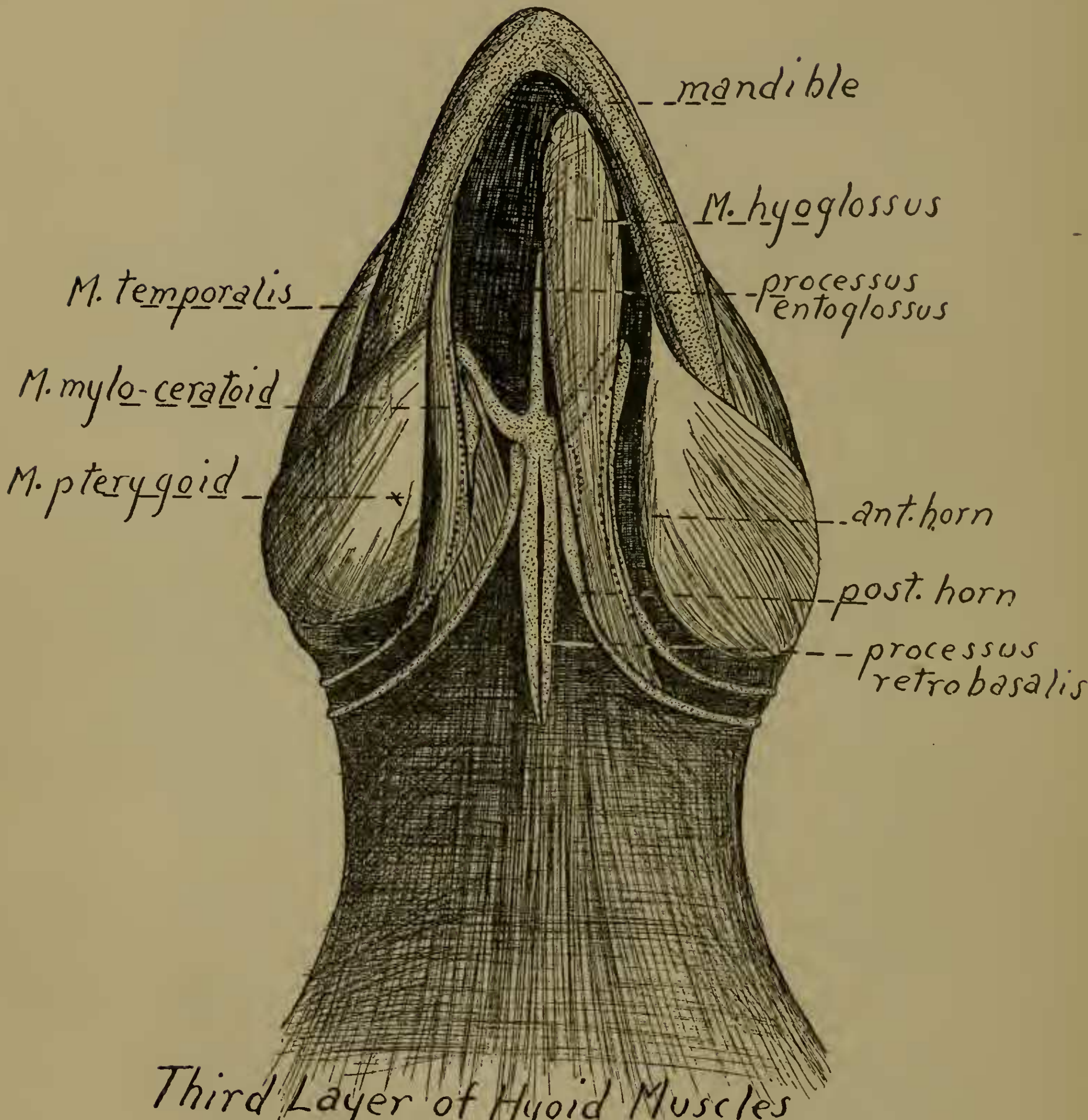

mandible
M. hyoglossus
processus entoglossus
M. temporalis
M. mylo-ceratoid
M. pterygoid
ant. horn
post. horn
processus retrobasalis
Third Layer of Hyoid Muscles

Fig. 7

the throat-fan in Anolis is independent of the swallowing of air, or any great ventral excursion of the basi-hyal. The hyoid apparatus in Anolis forms a lever of the first class while in Colotes, although not so stated by Chemin, it forms a lever of the second class. What Chemin calls the fulcrum, namely the basi-hyal, is not a fulcrum since this is the point where force is employed. The true fulcrum lies somewhere along the processus entoglossus.

CONCLUSIONS

1. The throat-fan of the *Anolis carolinensis* is distended when the animal is apparently undisturbed. It is also distended during various emotional states interpreted as anger, fear or sex impulses.

2. The throat-fan is produced by the hyoid apparatus. It is accomplished by the tapering processus retrobasalis, which swings vertrad and cephalad carrying a fold of skin before it. Since the distal portion of the retrobasalis is more flexible than the proximal portion, the semi-circular outline of the fan is produced. The thinness of the fan is due to the cohesion of the moist opposing surfaces of the fold of skin and to atmospheric pressure.

3. The hyoid apparatus may be compared to a lever in which the first part of the anterior horn acts as the power arm, the basi-hyal as the fulcrum and the processus retrobasalis as the long arm. The anterior and posterior horns act as lateral supports and when acted upon by the muscles, fix the fulcrum.

4. The power is produced by the cerato-hyoids, which exert force in a caudal direction and draws the short arm of the lever dorsad and caudad, which in turn causes the weight arm to move cephalad and ventrad. The fulcrum is fixed by the antagonistic action of the supra- and infra-hyoid group of muscles.

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SYNONYMS

1

M. Cerato. hyoideus. Bronn.
Cératoidïen latéral externe (Cuvier) Dumèril.
Cerato-hyoid. Sanders.
Céra-cératoïdien. Chemin.

2

M. Cerato-mandibularis. Bronn.
Cérato-maxillaire. Chemin.
Mylo-hyoideus. Sanders.
Mylo-cératoïdien. (Cuvier) Dumeril.
Seitwärtszieher des Zungenbeins. Meckel.
Mandibulo-hyoid.

3

M. Episterno-hyoideus sublimis. Bronn.
Sterno-hyoideus. Mivart, Sanders, Stannius.

Sterno-hyoidien. (Cuvier) Dumèril.
Niederzieher des Zungenbeins oder Brustbeinzungenbeinmuskels. Meckel.
Episterno-cleido-hyoideus sublimis; Fürbringer.
Sterno-cleido-hyoidien superficiel. (Chemin.)

4

M. Omo-hyoideus. Bronn.
Omo-hyoidien. (Cuvier) Duméril, Chemin.
Episterno-cleido-hyoideus sublimis. 2th. Fürbringer.
Omo-hyoid. Mivart, Sanders.
Omo-hyoideus, Stannius.
Rückwärtszieher des Zungenbeins oder Schulterblattzungenbeinmuskels. Meckel.

5

M. Mylo-ceratoideus. (Apparently hitherto unnamed.)

6

M. Mylohyoideus.
Mylo-hyoidien. (Cuvier.) Duméril.
Zwischenkiefermuskel. Meckel.
Mylo-hyoideus. Stannius.
Hyomandibulare. Sanders. (Platydactylus.)
Platysma myoides. Sanders. (Liolepis, Phrynsoma.)
Mylo-hyoideus and Platysma myoides. Mivart.

7

Genio-hyoid.
Cerato-génien. (Chemin.)